

REPRODUCTION IN THREE SPECIES OF INTERTIDAL BARNACLES FROM CENTRAL CALIFORNIA

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The reproductive biology of eastern Atlantic barnacles has been studied extensively, with emphasis on the role of temperature in regulating reproduction (*e.g.*, Crisp, 1950, 1954; Patel and Crisp, 1960a; Barnes, 1963; Barnes and Stone, 1973). However, there has been much less work on cirripedes elsewhere in the world. This paper compares the reproductive cycles and brood production of three species of intertidal barnacles abundant in central California: *Chthamalus fissus* Darwin, 1854; *Balanus glandula* Darwin, 1854; and *Tetraclita squamosa rubescens* Darwin, 1854 (hereafter called *T. squamosa* in this paper).

On the west coast of North America the role of barnacles in the structure of intertidal communities has been stressed (*e.g.*, Connell, 1970; Dayton, 1971), but the reproductive cycles of only two intertidal and one subtidal species have received attention. *Balanus glandula* from British Columbia and southern California broods primarily in the cold winter and spring months but may show minor brooding activity in summer (Barnes and Barnes, 1956). On the other hand, *Pollicipes polymerus* has a variable reproductive cycle with a limited summer brooding season in Washington which increases in length to central California (Hilgard, 1960; Lewis, 1975), while brooding activity in southern California peaks in winter with 30% still brooding in summer (Straughan, 1971). *Balanus pacificus*, a subtidal species in southern California, broods at high frequencies year-round showing no correlation with temperature (Hurley, 1973). Thus, in these species the relationship of reproduction with temperature is complex. The role of temperature or other environmental factors as proximal cues synchronizing brooding has not been studied experimentally in species of cirripedes on the west coast of North America.

In this paper brooding and nutrient storage cycles are compared in populations of the three species of barnacles occurring in the warm-water discharge canal of a large power plant and in adjacent areas of ambient temperature. Aspects of the regulation of these cycles by temperature, photoperiod, and food availability are investigated experimentally. The size and number of broods produced during a season are estimated so that the patterns of reproductive effort of these three species can be compared with other cirripedes.

MATERIALS AND METHODS

This study was conducted at the Pacific Gas and Electric Company fossil-fuel power plant at Morro Bay, California (35° 22' 30" N, 120° 52' 30" W). This 1030 megaWatt plant uses ocean water for once-through cooling, discharging a

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plume with an isotherm 5°C above ambient of about 0.6 to 3.0 acres surface area. Continuous temperature records (see Fig. 1) were taken from "Ryan" temperature recorders positioned next to the intake screens and the outfall next to the discharge tubes. Both recorders were at about mean lower low water, corresponding to the approximate intertidal level of the sampled barnacles.

Field data were gathered from populations of *Chthamalus fissus*, *Balanus glandula*, and *Tetraclita squamosa* occurring in the warm-water outfall and in adjacent control areas of ambient temperatures in the Morro Bay harbor channel. Collecting trips were made at about monthly intervals from November, 1972, to January, 1975. *C. fissus* is small (< 8 mm basal diameter) and common in the high intertidal Zone 1 of Ricketts and Calvin (1968) from San Francisco to Baja California. *B. glandula* grows to about 20 mm in diameter and is common in the upper mid-intertidal Zone 2 from Alaska to Baja California. *T. squamosa* attains a maximum diameter of 50–60 mm and is found in lower mid-intertidal Zone 3 from San Francisco to Baja California. Although these zonal distributions are characteristic, the three species are often found together in Zone 3, and every effort was made to collect samples from equivalent tidal levels (0 to +1.0 feet above mean lower low water) to minimize effects of differences in exposure and feeding time.

For each species, barnacles of haphazard sizes over the entire range available were selected for processing. Each barnacle was examined for brooded embryos, ripeness of ovary, and ripeness of the male reproductive system. Brooding frequencies were calculated for barnacles known to be reproductively mature. Ovaries were staged "ripe" when they had large quantities of yolky material bulging into the mantle chamber, or "not ripe" when little or no yolk was present. The male reproductive system was staged as "ripe" or "not ripe" according to the presence or absence of seminal vesicles discernibly filled with white seminal fluid. The basal diameter along the rostral-carinal axis and the following dry weights were determined for each barnacle: the opercular valves; the body (soma only, excluding ovary, retractor muscles, and tissue lining the mantle cavity); brooded egg mass; and, in some cases, the ovary (including retractor muscles and tissue lining the mantle cavity).

Egg numbers per brood were counted using a Model A Coulter Counter modified to count all the eggs in each brood. The eggs of each brood were dissociated with protease in sea water, fixed in formalin, and run through the counter. The length and width of a few eggs in each brood were recorded, as was the dry body weight of the parent.

For laboratory experiments barnacles were maintained on small rocks continuously submerged in vigorously aerated sea water under constant photoperiod and temperature conditions. Barnacles were fed *ad lib* with dense suspensions of *Artemia salina* nauplii, augmented in some cases with cultures of *Dunaliella* sp. All three species were maintained many months using these techniques. Temperature experiments were conducted at 11.5° or 20° C, representing winter ambient and outfall water temperatures, respectively. Photoperiods used represented the long (14L:10D), intermediate (12L:12D), and short (10L:14D) day-lengths occurring at Morro Bay.

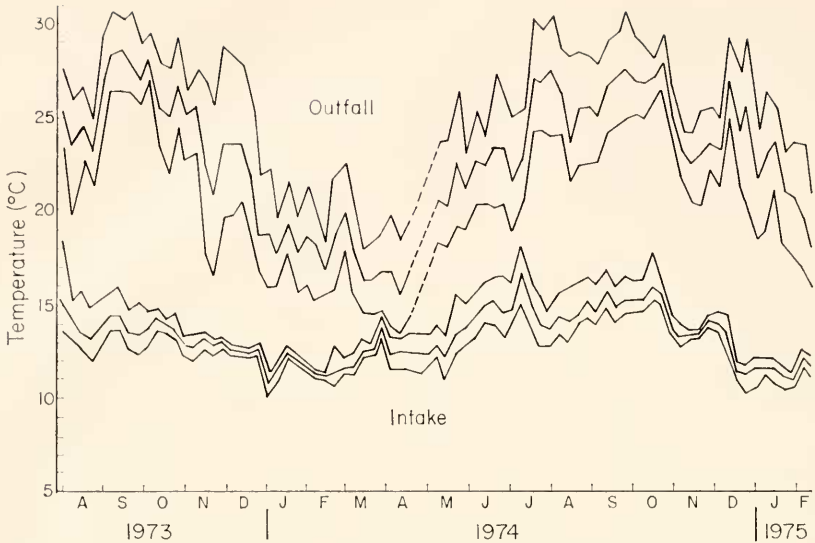


FIGURE 1. Temperature records for outfall and intake at Morro Bay power plant, plotting weekly high, mean, and low temperatures averaged from six-hour intervals. Recorders were positioned at about mean lower low water.

To estimate the length of time embryos were brooded, egg lamellae judged freshly deposited were removed from barnacles, broken into small clumps of embryos, and held in the laboratory under constant temperature and photoperiod until they hatched or reached late developmental stages judged ready to hatch. Sterilized sea water for these *in vitro* brooding-time experiments was treated with antibiotics, continuously aerated, and frequently changed.

RESULTS

Brooding cycles

Brooding frequencies for outfall and control populations of the three species are shown in Figure 2. The control populations of *Chthamalus fissus* brooded during a long summer season from about March or April to October. In peak periods from June to September, 50–75% of the sample were brooding, but low levels of about 10% brooding often occurred during the “off” season. Although the brooding frequencies of outfall and control samples of *C. fissus* were often quite different at any given month, there was no consistent difference in the overall brooding cycle timing or amplitude from the two areas. Broods in all developmental stages were found in both populations at all times of the year.

The control populations of *Balanus glandula* brooded embryos in winter and spring from about December or January to May, with about 60–80% of the control population brooding during peak months. Occasional low levels (about 5%) of brooding occurred in fall months, but the onset of the brooding cycle was abrupt. The samples from the warm-water outfall consistently had a lower percentage of

brooding, and the onset of brooding was delayed one or more months in both 1972-73 and 1974-75, but not in 1973-74. The samples at the onset of the brooding period each year showed a high frequency (about 95%) of broods in early developmental stages, suggesting that the deposition of the first brood was quite synchronous in both populations. Subsequent samples in the brooding season did not reflect any synchrony, and all developmental stages of brooded embryos were found.

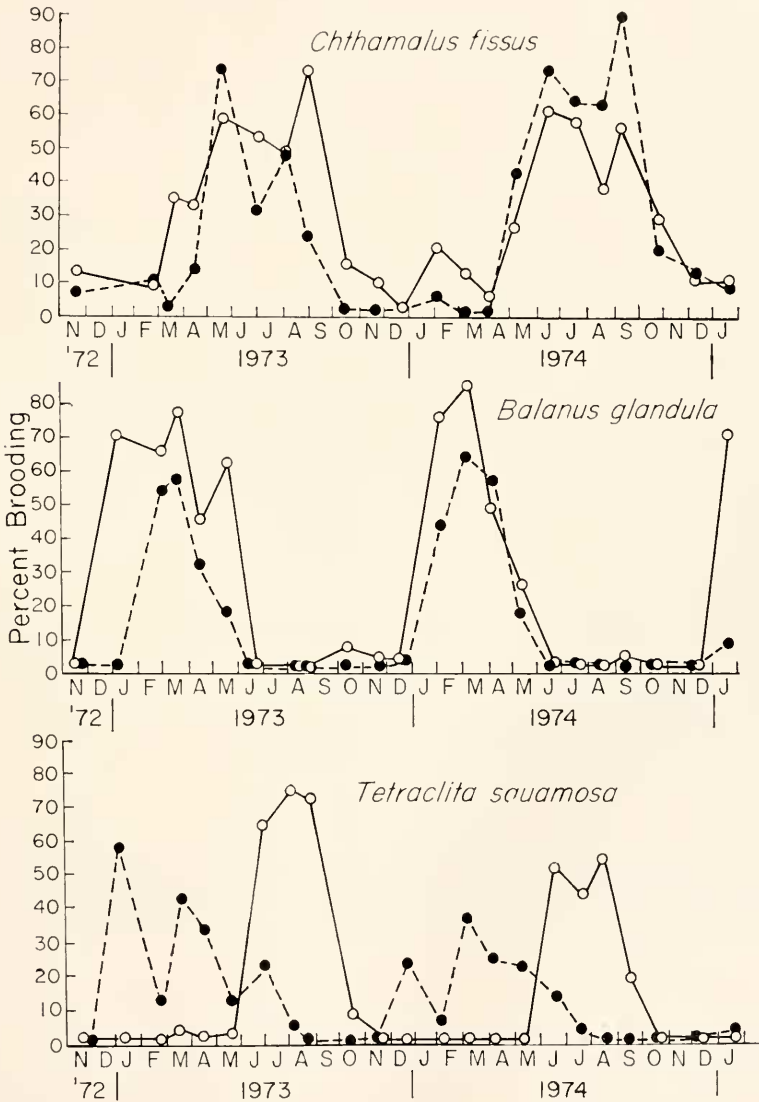


FIGURE 2. Cycles of brooding frequencies: outfall, solid symbols; control, open symbols. Sample sizes are: *Chthamalus fissus* = 50; *Balanus glandula* = 60; *Tetraclita squamosa* = 60 \geq 18 mm basal diameter.

The control population of *Tetraclita squamosa* brooded during summer from about June through September. The onset of brooding was sharp, and 40–75% of the population brooded embryos during peak months. The population in the warm-water outfall began brooding in or near December and continued at erratically variable levels through spring into early summer, diminishing in June or July when the control population was reaching peak activity. The brooding cycle of the outfall population was thus about six months out of phase with the control and more variable in activity, of longer duration but with lower peak brooding frequencies than the control population. Samples from the control population at the onset of the brooding season showed a high frequency (about 80%) of broods in early developmental stages, indicating a synchrony of deposition of the first brood. This synchrony was not found in subsequent samples in the season, and it was not found at all in the samples of the outfall population.

Brooding frequencies as a function of size were calculated for each species. There was no significant change in brooding activity with size in *Chthamalus fissus*; any individual above 2 mm basal diameter (about 2 months old; Hines, 1976) was judged to be mature. No individual of *Balanus glandula* less than 5 mm basal diameter was available for sampling during months of brooding activity, since they had all grown to at least that size by December (about 6 months old; Hines, 1976). Above 5 mm there was no significant change in brooding activity with size, so all individuals were considered mature by the time the populations began to brood in the winter. In *Tetraclita squamosa*, however, barnacles less than 6 mm basal diameter did not brood. They began to mature at about 12 mm, and became fully mature at about 18 mm in diameter (at about two years old; Hines, 1976). Above 18 mm in size there was no significant change in brooding activity.

Laboratory experiments on brooding

Comparisons of brooding cycles in the warm-water outfall and control populations suggested that for *Chthamalus fissus* temperature is not an important factor regulating brooding, since the cycles of the two populations are similar. In *Balanus glandula* the delayed and lower percentages of brooding in the outfall population suggested that temperature is important in regulating both the timing

TABLE I

Laboratory brooding experiment. Chthamalus fissus and Balanus glandula collected from both the outfall and control populations were maintained in the lab from October 12 to December 30, 1973; photoperiod, 12L:12D; food, Artemia nauplii fed ad lib; temperatures, 11.5° or 20° C. Brooding frequencies for the lab barnacles and the field populations at the end of the experiment are shown.

	11.5° C		20° C		Field 12/20/73	
	Control	Outfall	Control	Outfall	Control	Outfall
<i>Chthamalus fissus</i> N =	49% 58	42% 56	46% 38	40% 62	14% 50	13% 50
<i>Balanus glandula</i> N =	75% 77	61% 76	10% 80	8% 80	0% 60	0% 60

TABLE II

Laboratory brooding experiment on *Chthamalus fissus* maintained in the laboratory from September 17 to October 28, 1974: photoperiod, 12L:12D; temperature, 12° C. Brooding frequencies as a function of increasing food doses of *Artemia salina* nauplii are shown.

Food dose (ml)	0	10	31	58	100
Brooding (%)	15	18	33	48	74
N	103	66	98	87	66

and intensity of brooding, and that cold temperature is necessary for reproduction to proceed normally. In *Tetraclita squamosa* the pronounced shift in the brooding cycle of the outfall population suggested that temperature is important in regulating reproduction in this species also, but that warm temperatures are required for reproduction. A series of laboratory experiments was conducted to test these hypotheses and to investigate more fully the roles of temperature, photoperiod, and food availability in regulating reproduction. Results of these experiments will only be summarized here; further details and complete data are available from Hines (1976).

Brooding in *Chthamalus fissus* is regulated directly by food availability, and feeding with *Artemia salina* nauplii in the laboratory elicited high brooding frequencies (Table I) during periods when brooding activity and food levels in the field were low (Icanberry and Adams, 1974). The increased brooding response to food in the laboratory was rapid (within about 2 weeks), and the frequency of brooding was directly proportional to the size of the food dosage (Table II). Temperature (11.5° or 20° C) and photoperiod (10L:14D, 12L:12D, or 14L:10D) did not affect brooding in *C. fissus* in the laboratory during any season. For *Balanus glandula* cold temperature (11.5° C) induced early brooding in the laboratory during late fall and early winter, and warm temperatures (20° C) tended to inhibit it (Table I). However, cold temperature in the laboratory did not induce brooding in late summer to early fall even though *B. glandula* appeared ripe then; nor did cold temperature in the laboratory extend the brooding period into summer. Photoperiod (10L:14D, 12L:12D, 14L:10D) did not affect brooding activity during any season in *B. glandula*. Although the 6-month shift in the brooding cycle of *Tetraclita squamosa* in the outfall population strongly suggests that warm temperatures stimulate brooding, *T. squamosa* did not brood in the laboratory under any of the conditions tested (combinations of 11.5° or 20° C with 10L:14D, 12L:12D, 14L:10D and several food regimes), even during the time the field populations were brooding. Individuals appeared ripe with yolk in the laboratory, but the stimulus for brooding seemed missing.

Brood and egg size

Regressions of dry brood weight vs. dry body weight with 95% confidence intervals for slopes and intercepts are: *C. fissus*: $y = (0.718 \pm 0.039) \times + (0.035 \pm 0.030)$, $n = 391$, $r = +0.855$; *B. glandula*: $y = (1.58 \pm 0.093) \times - (0.962 \pm 0.526)$, $n = 363$; $r = +0.868$; and *T. squamosa*: $y = (1.21 \pm 0.066) \times - (8.86 \pm 1.82)$, $n = 248$, $r = +0.908$. Brood weight is quite variable in all three species;

however, there was no significant difference in brood weight/body weight regressions between outfall and control population or between broods occurring early or late in the respective brooding season of any of the three species (slopes and intercepts are not different at the 0.20 level). Because brood weight is positively correlated with body size and because there is a large size range of barnacles both within each species and between species, the slope of these regressions is taken as a relative measure of the brood size for each species. By this measure *Balanus glandula* has the largest relative brood size (1.58); *Tetraclita squamosa* puts out an intermediate brood (1.21); and *Chthamalus fissus* has a comparatively small brood (0.718).

Numbers of eggs in thousands per brood as a function of dry body weight are given in the following regressions showing the standard errors of the slopes and intercepts: *C. fissus*: $y = 2.54 (\pm 0.34) \times - 0.28 (\pm 0.27)$, $n = 24$, $r = 0.85$; *B. glandula*: $y = 1.72 (\pm 0.13) \times - 0.37 (\pm 0.98)$, $n = 33$, $r = 0.92$; and *T. squamosa*: $y = 0.75 (\pm 0.08) \times - 2.05 (\pm 1.15)$, $n = 33$, $r = 0.87$.

Size of the ovoid-shaped eggs of each species are given by their length and width at the first naupliar stage before hatching: $130 \times 95 \mu$ for *Chthamalus fissus*; $245 \times 175 \mu$ for *Balanus glandula*; and $340 \times 195 \mu$ for *Tetraclita squamosa*. These dimensions varied only by about $\pm 5 \mu$ within each species.

Body weight relative to opercular weight

The regressions of body weight relative to opercular valve weight for each outfall and control sample were computed. The intercepts of all these regressions were all near zero, and changes in the slopes were interpreted as measures of fluctuations in body weights of the barnacles. The body weights of the three species fluctuated erratically throughout the year, but there was no discernible seasonal cycle of body weight for any of the three species (Fig. 3). The control samples had consistently higher body weight to opercular valve weight ratios than outfall samples for all three species, except for the second year of data for *Balanus glandula* where there was no difference between the two populations. The body weights are not large compared to brood weight in all species, and it is hard to see how any sizeable quantity of nutrients could be stored there. Variability of body weights in monthly samples may reflect differences other than stored nutrients, e.g., gut contents. Furthermore, differences between outfall and control samples could have been due to differences in opercular valve weights. Because the opercular valves are much heavier than the bodies, small increases in calcium deposition at the higher temperatures in the outfall could have accounted for the smaller body weight to opercular valve weight ratios. The body weight cycles did not correlate with cycles of male reproductive systems of any of the species. It was therefore decided that body weights do not provide good reflections of nutrient storage patterns for these three species.

Male reproductive system

Cycles of the male reproductive systems of the three species are shown in Figure 4. Nearly all specimens of *Chthamalus fissus* have ripe male reproductive tracts

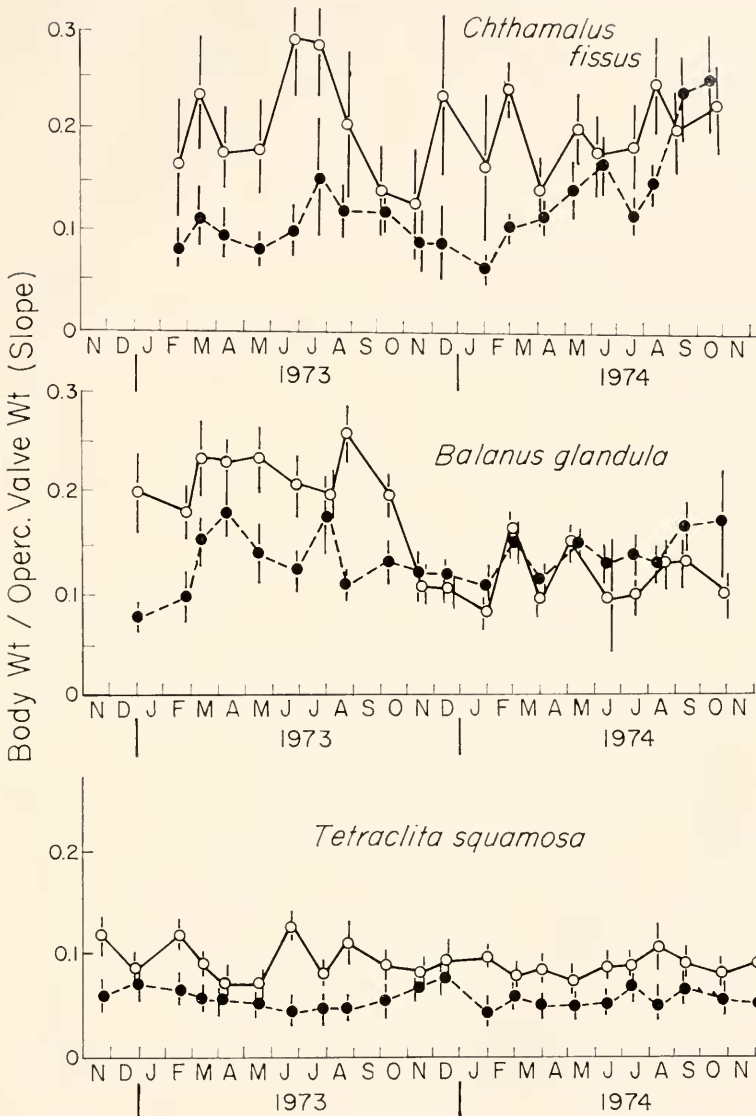


FIGURE 3. Body weight fluctuations. Slopes and 95% confidence limits for regressions of body weight versus opercular valve weight are plotted. Outfall population is represented by solid symbols; control population, open symbols.

year-round, with no significant difference between outfall and control populations. *Balanus glandula* had a definite cycle of the male system, developing in the fall from September to November, remaining ripe during the brooding season from December to May, and rapidly becoming quiescent in summer from June to August. Both populations were very synchronous and similar each year, although the control

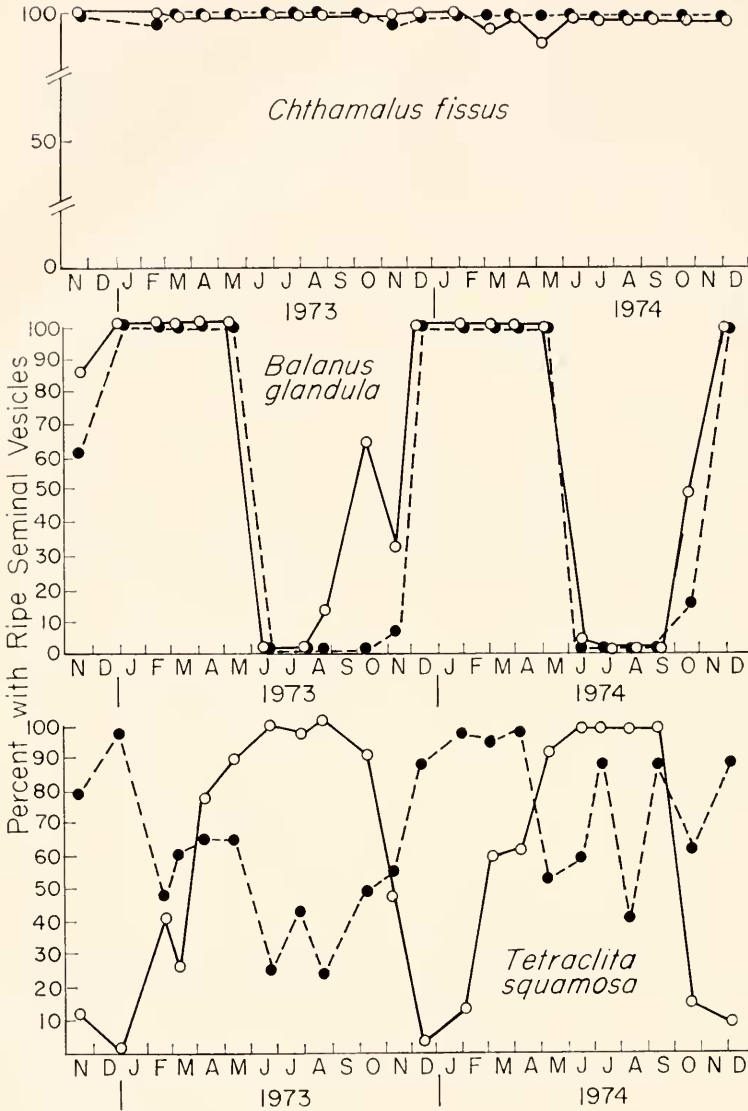


FIGURE 4. Cycles of male reproductive systems: outfall, solid symbols; control, open symbols. Sample sizes are: *Chthamalus fissus* = 50; *Balanus glandula* and *Tetracitla squamosa* = 60.

population became ripe slightly in advance of the outfall population. In *Tetracitla squamosa* the control population showed a distinct cycle of the male system with peak activity occurring from about April to October and low frequencies of ripe individuals from November to February, when development of the male tracts began again. In contrast, the outfall population tended to be at peak frequencies

of ripeness during winter, with erratic intermediate levels of activity during the rest of the year. The warm-water outfall obviously had a major disruptive effect on the cycle of development of the male system in this species.

Ovarian cycles and ovary weight-body weight regressions

Cycles of ovarian ripeness are shown in Figure 5. Ovarian development in *Chthamalus fissus* showed the same cycle as that of brooding frequency, except that

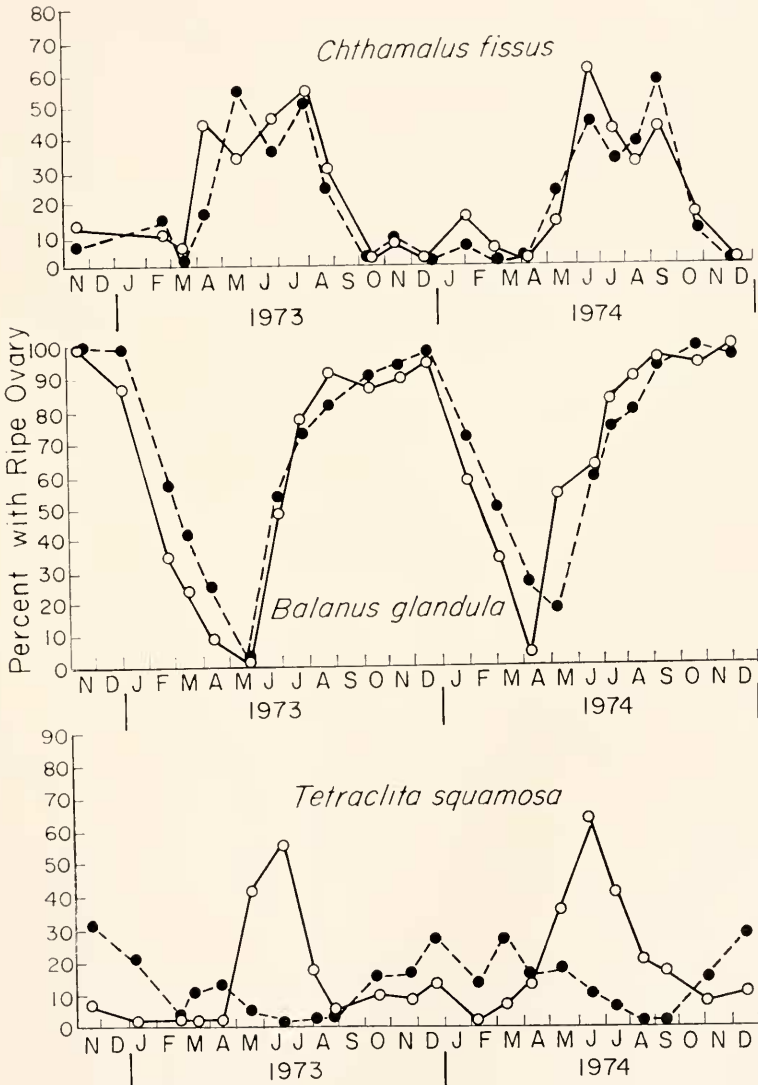


FIGURE 5. Ovarian cycles: outfall, solid symbols; control, open symbols. Sample sizes are: *Chthamalus fissus* = 50; *Balanus glandula* and *Tetraclita squamosa* = 60.

the summer peaks in ovary development did not reach as high frequencies. As in brooding frequencies, there were no consistent differences between outfall and control cycles of ovarian ripeness. The ovaries of *Balanus glandula* ripened rapidly in the summer from June to August. Nearly the whole population was ripe from August through December or January when brooding began. The frequencies of ripe individuals dropped during the brooding period to a low in April and May. The cycles for outfall and control populations were nearly identical, except that the control population appeared to have spent its ovaries somewhat in advance of the outfall population, which might be expected since it began brooding sooner. The ovarian cycle of the control population of *Tetraclita squamosa* showed that these barnacles became ripe in the late spring from April to May, slightly in advance of the brooding period, and percentages of ripe individuals dropped precipitously in July and August when the summer brooding peak was reached. Peak frequencies of ripe individuals roughly corresponded to the peak brooding frequencies attained. However, the warm-water outfall population had only low frequencies of ripe ovaries during a long period from October to May or June, encompassing the same time as the brooding period. This population had virtually no ripe individuals in the summer months.

To estimate the number of broods for which the ovary stored nutrients, ovary weights were analyzed during months when each species was maximally ripe (June, 1973, for *Chthamalus fissus*; December, 1973, for *Balanus glandula*; and June, 1974, for the *Tetraclita squamosa* control population), and also during months when they were least ripe (December, 1973, for *C. fissus*; May, 1973, for *B. glandula*; and

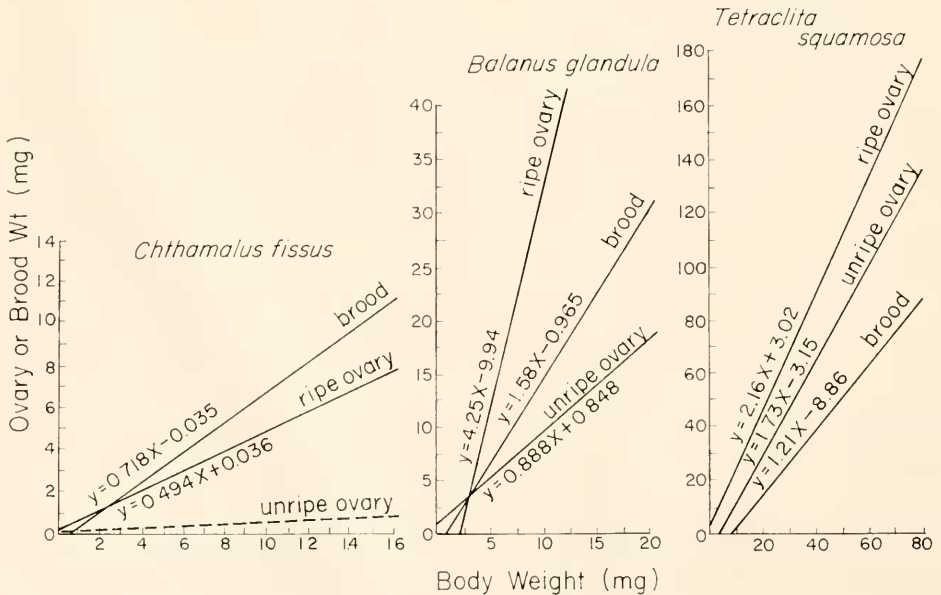


FIGURE 6. Regressions of ripe ovary weight, unripe ovary weight, and brood weight *versus* body weight. See text for further explanation.

February, 1974, for *T. squamosa* controls). The latter series of ovary weights were used as a baseline for "unripe ovary weight", because some of the "ovary" was actually retractor muscles and tissue lining the mantle chamber. Ripe ovaries are extremely diffuse and ramify through the compartment walls, so that some ovarian tissue always remained uncollected when scraped out for weighing. The regressions for "ripe" and "unripe" ovary weight *versus* body weight, as well as the brood weight *versus* body weight regressions, are shown in Figure 6. In *C. fissus* the unripe ovary was essentially nonexistent, and no tissue could be collected for weighing; as the ovary ripened, it increased up to a weight about equal to the brood size, indicating that not more than one brood was prepared at a time. In *B. glandula* the unripe ovary and associated tissues were significant in size and the ovary showed an increase of about 2.5 times the brood weight when ripe. This indicated that yolky material for a minimum of three broods and possibly more was stored in the ovary, considering that much yolky ovarian tissue was left behind in the shell during collection. In *T. squamosa* although both ripe and unripe ovaries and the associated tissues weighed more than the brood, ripe ovaries were only slightly larger than unripe ovaries. Therefore, although these tissues were potentially sizeable storage areas in *T. squamosa*, not much nutrient storage in the form of yolky material detectable by weight-change actually occurred—at most one brood was prepared in advance.

Time per brood and number of broods per season

Preliminary estimates of the time each brood was retained in the mantle chamber were made for *Chthamalus fissus* and *Balanus glandula* by keeping barnacles moist, but not submerged, in a 12° C cold room. Periodic samples of barnacles were inspected for the developmental stages of brooded embryos. Since copulation did not occur and no new broods were laid down unless the barnacles were submerged, only already existing broods continued to develop without hatching. In *C. fissus*, 100% of the broods were judged ready to hatch in about two weeks. In *B. glandula*, all broods were ready to hatch after one month, but the adults were in poor condition after this much time without submergence. *Tetraclita squamosa* could not be maintained unsubmerged for any extended period.

Patel and Crisp (1960b) showed that brooding time determined *in vitro* corresponded well with *in vivo* times for several species of barnacles. To get a better estimate of the time per brood, freshly deposited eggs were removed from the mantle chambers of each species and maintained *in vitro*. *C. fissus* nauplii did not hatch *in vitro* but development appeared to continue normally to a darkly pigmented, eyed nauplius stage which was judged ready to hatch by comparison with the most advanced embryos brooded in the field. The reason hatching did not occur is not known, and whether the proper stimulus required parental presence, or some environmental factor, or both, was not investigated. At 12° C, *C. fissus* nauplii were judged to be ready to hatch in 14 days (s.d. = ± 3 days; n = 21 broods). At 19° C development time for *C. fissus* was 12 days (s.d. = ± 2 days; n = 15 broods). Embryos of *B. glandula* readily developed and hatched *in vitro*. At 12° C time to hatching was 27 days (s.d. = ± 6 days; n = 24 broods), and at 19° C *B. glandula* hatched in 22 days (s.d. = ± 4 days; n = 15 broods). *T. squamosa*

TABLE III

Reproductive effort estimated as the yearly weight allocation to egg production. Length of brooding season divided by the incubation time per brood is the maximum number of broods per year. The number of broods per year times the slope of the brood weight versus body weight regression is brood weight/body weight per year.

	<i>Chthamalus fissus</i>	<i>Balanus glandula</i>	<i>Tetraclita squamosa</i>
Length of season	8 months	6 months	4.5 months
Time per brood	0.5 month	1 month	1.5 months
Maximum number broods per year	16	6	3
Brood wt/body wt	0.718	1.58	1.21
Brood wt/body wt per year	11.49	9.48	3.63

nauplii hatched in 40 days (s.d. = ± 8 days; $n = 20$ broods) at 12°C and 30 days (s.d. = ± 7 days; $n = 13$ broods) at 19°C . In summary, "normal brooding time" (i.e., at 12°C) was estimated at about 0.5 months for *C. fissus* ($Q_{10} = 1.25$); 1.0 month for *B. glandula* ($Q_{10} = 1.34$); and 1.5 months for *T. squamosa* ($Q_{10} = 1.51$).

To calculate a maximum number of broods per year produced by the control populations of each species, the length of the brooding season was divided by the estimated time required for each brood, yielding about 16 broods per season for *Chthamalus fissus*, six for *Balanus glandula*, and three for *Tetraclita squamosa* (see Table III). This calculation makes the assumption that there is no delay between broods. Probably at least a short period between broods in fact occurs, because less than 100% of the barnacles were brooding at any given time. However, there is strong circumstantial evidence that each species puts out several broods in rapid succession, as shown by Crisp and Davies (1955) and Patel and Crisp (1960a, b) for other species. The length of the brooding season for each species in the present study was clearly much longer than the developmental time for each brood, and most barnacles had ripe ovaries remaining while still brooding. Embryos of all stages of development were found throughout the brooding season of each species, and occasionally a new brood was present while advanced embryos from a previous brood remained. Thus, the assumption that there was minimal delay between broods appears reasonable.

Any delay between broods would tend to decrease the number of broods produced in a season. For example, a lag of only 4–5 days between broods in *Balanus glandula* would reduce from six to five the estimate of the number of broods produced over the 6-month season, and this short lag could result in 15–20% of the population not brooding at any given time. On the other hand, any factor, such as temperature higher than 12°C , which shortens the brooding time would tend to make the production of more broods possible. It is thus very difficult to estimate the number of broods produced by the outfall populations. *B. glandula*, for example, tends to have a delayed, shorter brooding season in the outfall with a lower percentage of the population brooding at any given time, but the higher temperatures probably shorten the time each brood is retained. *B. glandula* in the control population thus produces a minimum (based on storage) of three and a maximum (based on brooding time) of six broods per season. It is difficult to estimate a

minimum number of broods per season for *Chthamalus fissus* and *Tetraclita squamosa*, because they do not store yolk for more than one brood at a time.

Patterns of nutrient storage and reproductive effort

A schematic model of the patterns of nutrient storage during the year is presented in Figure 7, showing proportional changes in ovary size relative to brood size for each species. Broods in *Chthamalus fissus* are deposited as soon as enough nutrients are accumulated. As plankton production increases during spring and

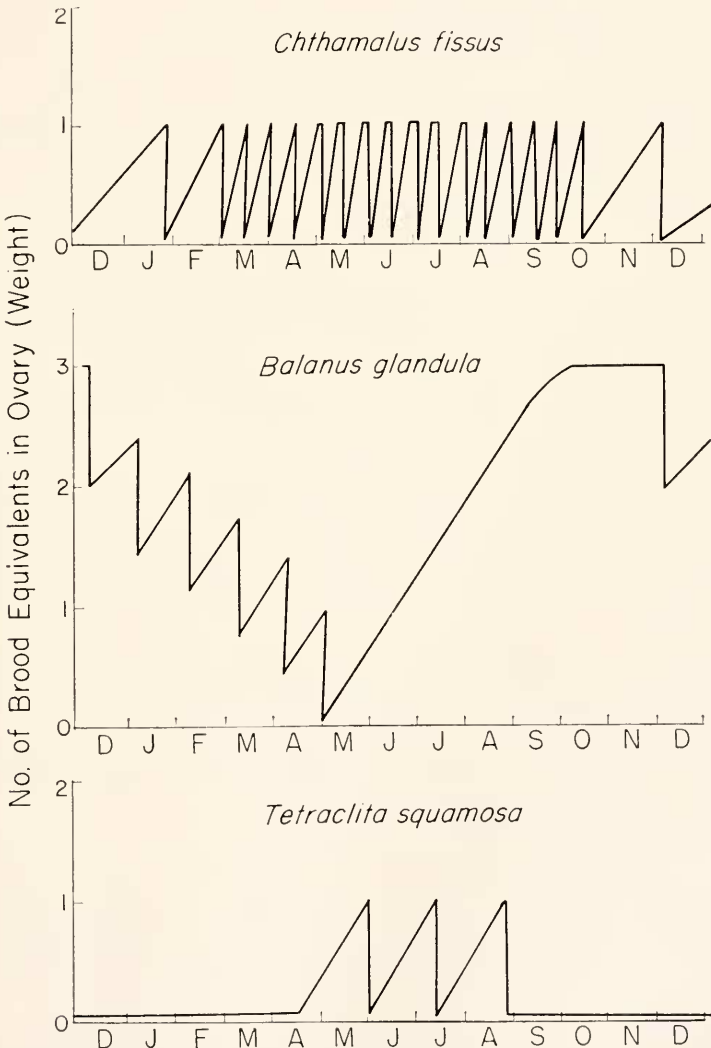


FIGURE 7. Schematic model of patterns of nutrient storage in ovary. Amount of yolky material equivalent to the weight of a brood is shown over a one year cycle for each species.

summer, the rate of yolk accumulation increases and broods are produced more frequently, until brood production is limited by the time required for brood incubation. In contrast, *Balanus glandula* rapidly stores nutrients for at least three broods during the summer and remains ripe until cold temperatures induce brooding. As broods are released during winter and spring, more nutrients are probably added as the barnacles feed until they are spawned out in May after up to six broods. *Tetraclita squamosa* produces only three broods in the summer, and only yolk for one brood at a time is accumulated.

Comparisons of the reproductive efforts of the three species estimated as brood weight relative to body weight per year are shown in Table III. For each species the estimated maximum number of broods produced per season is multiplied by the slope of the regression of brood weight on body weight to calculate the total size-specific brood weight expended during the year. *Chthamalus fissus* has the highest proportional reproductive effort—11.49 times the body weight produced as broods; *Balanus glandula* expends an intermediate but large amount—9.48 times the body weight; and *Tetraclita squamosa* has the lowest weight allocation to brood production—3.63 times the body weight.

DISCUSSION

Species of barnacles may be grouped into roughly five categories based on a spectrum of reproductive patterns: first, a boreo-arctic pattern in which a single large brood is incubated over winter; secondly, a pattern shown by a few cold-temperature species which produce a small number of broods in winter and spring; thirdly, a variable pattern found in several warm-temperature and subtropical species which produce many small broods during summer; fourthly, a possibly different summer pattern of producing only a few broods, as demonstrated here by *Tetraclita squamosa*; and fifthly, a pattern of brooding throughout the year. Some species may show different patterns of reproduction in different parts of their geographic range.

The boreo-arctic species *Balanus hameri*, *B. balanus*, and especially *B. balanoides* are perhaps the best understood and have the most precisely timed, least complex pattern of brood production. These barnacles store nutrients during a refractory summer period when brooding cannot be induced (Barnes, 1963). In *B. balanoides* copulation occurs in late fall, cued by a low temperature threshold modified by photoperiod (Barnes, 1963), and in *B. balanus* and *B. hameri* copulation occurs in mid-winter (Crisp, 1954; Barnes and Barnes, 1954). A single large brood is incubated over winter, and naupliar release is synchronized with the spring diatom bloom by chemical agents produced by the parents and/or the diatoms (Crisp, 1956; Barnes, 1957). Clearly, the adaptive significance of this precise timing is based on the predictability of the marked seasonal changes in temperature, photoperiod, and productivity of northern latitudes.

Verruca stroemia and *Balanus glandula* in cold temperate waters exemplify a different pattern of brood production during winter and spring. *V. stroemia* is similar to the boreo-arctic species in that it produces a major brood in the winter which is synchronous throughout the whole population, and which is released about

the time of the spring diatom increase (Barnes and Stone, 1973). However, unlike the boreo-arctic species, minor broods are subsequently produced asynchronously during spring and summer. Barnes and Barnes (1956) found brooding cycles for *B. glandula* at British Columbia and southern California similar to that reported here for central California. The northern population showed a shorter period of high brooding frequency from January to March, with low frequencies occurring erratically during spring and summer, while their southern population showed a broader season of high brooding frequencies from November to May. The length of the season reported here for Morro Bay is intermediate from December or January to May. Since the present laboratory experiments and the delay of brooding in the warm-water outfall clearly show that the initiation of brooding in *B. glandula* is regulated by cold temperature, the longer brooding season of the southern populations is hard to explain. The brooding season of the Morro Bay population was not extended with laboratory manipulations. In any case, based on cycles of brooding frequency, Barnes and Barnes (1956) suggest *B. glandula*, like *V. stroemia*, produces a single major winter brood followed by a second minor brood in spring. At Morro Bay at least three and as many as six broods are produced, with the first being nearly synchronous in winter and the others following at about monthly intervals through spring. This pattern apparently times the settlement of many larvae in late spring and early summer, when warming temperatures and high food availability are optimal for growth (Hines, 1976), and this pattern distributes the chance of reproductive success over several broods.

Several species of cirripedes in warm-temperate and subtropical regions characteristically produce numerous small broods in rapid succession during summer. The length of the brooding season is usually broadly defined by temperature, and during the season the production of broods is only limited by food availability for restoring the ovary and by the temperature-dependent development rate of the brood in the mantle chamber (Crisp, 1950; Patel and Crisp, 1960a, b). The incubation time per brood as a function of temperature has been measured for a number of species (Patel and Crisp, 1960b), allowing a calculation of about 13–22 broods produced in *Chthamalus stellatus* and 10–25 broods in *Balanus amphitrite denticulata* during spring and summer. *C. fissus* in the present study produces about 16 broods. Although its brooding season is limited by food availability rather than temperature, its reproductive pattern fits in this category. This seasonal pattern is adaptive for quick, opportunistic response to short-term changes in the environment, while minimizing the energetic cost of any single brood if conditions turn bad. It also disperses sibling larvae and improves chances of colonization (Strathmann, 1974).

In the present study *Tetraclita squamosa* produces only about three broods in summer, each incubated for a long period. This is contrary to the pattern in which those species that reproduce in summer tend to produce numerous, frequent broods, while those that put only a few broods seem to be northern species which breed in winter and/or spring. The early reproduction of *T. squamosa* in the warm-water outfall strongly suggests that brooding is cued by warm temperature, although further study is needed since brooding of this species could not be induced in the laboratory. *T. squamosa* grows to a size large enough to attain immunity from

many predators and compete successfully for space at low tidal levels (Hines, 1976). It does not become reproductively mature until it has grown to about 18 mm in diameter, and brooding occurs during the productive summer period. This would minimize the amount of energy diverted from growth to reproduction during critical periods of small size and low food availability.

Elminius modestus and *Balanus pacificus* brood continuously year-round, and both species grow and become reproductively mature very quickly (Crisp and Davies, 1955; Hurley, 1973). *E. modestus* produces a brood about every two weeks during summer; but the rate of brood production is markedly reduced during the cold winter months when food availability is low, resulting in about 12–20 broods per year. *B. pacificus* produces about 23–33 broods per year with no obvious seasonal cycle. Both species are characterized as colonizers, with *E. modestus* undergoing a rapid range expansion since its introduction in Europe and *B. pacificus* settling subtidally on newly bared substrate (Crisp and Davies, 1955; Hurley, 1973).

Some species of cirripedes with wide latitudinal distributions exhibit variable reproductive cycles. For example, *Pollicipes polymerus* shows a variable reproductive season from Washington to southern California. The northern populations brood in summer (Lewis, 1975), and the length of the season increases to the south in northern and central California (Hilgard, 1960; C. Hand, J. Standing and J. Rutherford, personal communication). Farther south at Morro Bay brooding occurs at erratically high frequencies year-round (Hines, unpublished), and at Santa Barbara in southern California peak brooding activity occurs in the winter with at least a 30% brooding frequency in the summer (Straughan, 1971). *Balanus amphitrite denticulata* has a brooding season limited by temperature from June to August in Great Britain (Patel and Crisp, 1960b), while the brooding of *B. amphitrite communis* in India appears restricted from September to June by salinity and food availability (Pillay and Nair, 1972). *Balanus crenatus* in northern British waters has a boreo-arctic pattern of producing a single large winter brood (Barnes and Barnes, 1968), but it may produce a second, spring brood elsewhere in Great Britain (Patel and Crisp, 1960b), while subtidal populations in central California produce numerous small broods year-round with no obvious seasonal cycle (personal observations). These species with variable reproductive cycles deserve much more study, because they may provide valuable insights into the way proximal environmental cues regulate reproduction under different conditions.

Comparisons of reproductive effort in barnacles require estimates of both the size as well as number of broods produced per year. Because published data on brood weights for barnacles have not been available before the present paper, Barnes and Barnes (1968) compared relative brood volumes of a variety of barnacle species as a next best indicator of brood size. For each species they calculate a product (NV) as a measure of the brood volume relative to the size of the barnacle. ("N" is the increase in numbers of eggs per brood per 50 micrograms dry body weight and "V" is the volume in 10^{-6} ml of an ellipsoid calculated from the length and width of the "egg" at the first naupliar stage.) Brood sizes of barnacles from their calculations fall into three categories: first, boreo-arctic species (including *B. balanoides*, *B. balanus*, and *B. crenatus*) with very large broods, $NV = 1500\text{--}3500$; secondly,

temperate and subtropical species (including five species of *Balanus*, two species of *Chthamalus*, and one each of *Octomerus*, *Tetraclita*, and *Elminius*) with intermediate but much smaller broods, $NV = 100-500$; and thirdly, a few species (including two species of *Pollicipes*, one *Chthamalus* and one *Verruca*) with very small broods, $NV = 30-60$. From their data, *B. glandula* ($NV = 292$) is included in the second group and *C. fissus* ($NV = 47$) is in the third; no data are given for *T. squamosa*. From the regression of egg numbers per brood versus dry body weight and from the dimensions of the eggs for the Morro Bay populations, comparable NV values can be calculated for *C. fissus* (61) and *B. glandula* (265), and an additional value for *T. squamosa* (199).

Barnes and Barnes (1968) proposes the product (NVB) of the number of broods produced per year (B) times the NV value of a species. They suggest that since boreo-arctic species produce only a single brood and warm-water species many broods, NVB values are roughly equal for all species and the "metabolic efficiency of egg production" in barnacles is constant. However, without measurements of the amount of food available to different species and calculations of their assimilation rates and energy budgets, the term "metabolic efficiency" is misleading, and "reproductive output" or "reproductive effort" are better terms to describe the data. The reproductive efforts of the Morro Bay populations computed similarly as a function of volume are: $NVB = 979$ for 16 broods in *Chthamalus fissus*; $NVB = 1589$ for six broods and 795 for three broods in *Balanus glandula*; and $NVB = 597$ for three broods in *Tetraclita squamosa*. By this measure *B. glandula* has the largest reproductive output of the three species. This ranking does not correspond with the estimates of yearly weight allocation to eggs presented here, although at only three broods per year *B. glandula* would be intermediate between *C. fissus* and *T. squamosa*. Moreover, neither these NVB values nor the estimates of reproductive effort based on weight support the hypothesis that the relative reproductive output of barnacles is constant. Although the NVB value for *B. glandula* at six broods per year is in the low range of values for boreo-arctic species, *C. fissus* would have to produce eight and *T. squamosa* four to five additional broods per year to approach the NVB values of *B. balanus* or *B. crenatus*. In fact, the constancy of reproductive effort proposed for barnacles would not be expected (see Stearns, 1976). In species which produce many small broods small NVB variations would be equivalent to a difference of a brood or two, and this may be very significant ecologically. The unanswered critical questions center on why boreo-arctic species have such a very large reproductive output and on the environmental causes for small, but important variations in reproductive effort in barnacles.

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SUMMARY

1. The reproductive cycles and brood production of *Chthamalus fissus*, *Balanus glandula* and *Tetraclita squamosa* from central California are compared. *C. fissus* produces about 16 small broods from March through October. *B. glandula* produces three to six relatively large broods from December or January to May. *T. squamosa* incubates only about three intermediate-sized broods from June through September.

2. Brooding in *C. fissus* is regulated by food availability, and yolk for no more than one brood is stored at a time. Feeding in the laboratory elicited high brooding frequencies during periods when brooding activity and food levels in the field were low, and the frequency of brooding was directly proportional to the size of the food dosage. Temperature and photoperiod did not affect brooding frequencies. *B. glandula* rapidly stores nutrients in the ovary for about three broods during summer. Cold temperatures induce early brooding in the laboratory during late fall and early winter, and the population in the warm-water outfall showed delayed and lower brooding frequencies. Photoperiod did not affect brooding in *B. glandula*. *T. squamosa* in the warm-water outfall brooded six months earlier than the control population, suggesting warm temperatures are required for reproduction. Yolk for only one brood at a time is stored in *T. squamosa*.

3. Comparisons of reproductive efforts estimated as brood weight relative to body weight per year show that *C. fissus* has proportionally the largest brood production; *B. glandula* an intermediate but large amount; and *T. squamosa* the smallest reproductive output.

4. It is proposed that species of barnacles may be grouped into five categories based on major patterns of reproductive timing and brood production. The three species in the present paper show three of these patterns. The reproductive effort of these three species is compared with other cirripedes.

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